

SIZE VARIABILITY IN THE WORKER CASTE OF A
SOCIAL INSECT (*VEROMESSOR PERGANDEI* MAYR) AS A
FUNCTION OF THE COMPETITIVE ENVIRONMENT

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The most convincing evidence for the importance of competition in structuring natural communities is the documentation that a species' utilization of resources varies in relation to its competitive environment. Such "niche shifts" are often, though not always, associated with morphological change. In resource-limited communities, coexisting competitors frequently subdivide resources on the basis of food type, microhabitat, or some other dimension(s) (Grinnell [1917], Crombie [1946], reviewed in Schoener [1974] for natural communities). The same species may utilize broader ranges of resources in habitats where the intensity of competition is significantly reduced. Islands often constitute such habitats, and "niche expansion," or "competitive release," has been reported for insular populations of a number of organisms (e.g., Brown and Wilson 1959; Wilson 1961; Crowell 1962; Schoener 1967, 1975; and MacArthur et al. 1972). Although relatively contiguous habitats on continents may also differ in the number of coexisting competitors, there have been fewer demonstrations of competitive release in this context (but see Brown 1975 and Cody 1975).

The potential for competitive release exists at several levels (Van Valen 1965; Roughgarden 1972). It may take the form of (1) immediately increased phenotypic plasticity, including behavioral responses (Werner and Hall 1976); (2) evolutionary change in the variance of resources utilized by individual phenotypes; and (3) evolutionary change in the variance of phenotypes in the population (Van Valen 1965; Grant et al. 1976). In attempting to determine the general importance of genetic variation among individuals in a population as a response to competition, investigators frequently have evaluated morphological variation among individuals and tried to correlate this variability with known or purported measurements of niche breadth (Van Valen 1965; Soulé and Stewart 1970) or with the number of coexisting competitors (Schoener 1967; Willson 1969; Rothstein 1973). However, in many cases the relationships between morphology and inferred niche parameters remain undocumented. In this paper, I directly relate morphology to resource utilization in order to evaluate the ecological and evolutionary significance of size variability in worker ants.

The social Hymenoptera are especially interesting subjects for studies of character release because their unique capacity to express polymorphism at the level of individual workers within a colony provides the potential for extremely fine tuning to the competitive environment. Wilson (1968) first suggested that caste ratios in social insects are subject to selection acting at the colony level and that the observed caste ratios are those which maximize the production of reproductives. More recently, Oster et al.

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(1977) have derived an expression for the inclusive fitnesses of workers and queens and proposed that optimal investment of colony resources in the various castes should occur when this quantity is maximized subject to ergonomic constraints. These constraints may include the number and distinctness of the challenges facing the colony, the temporal pattern of fluctuations in the frequency and importance of the challenges, the costs of failure to meet these contingencies, and the relative efficiencies of the different castes in performing the tasks (Wilson 1968). Some or all of these factors may be expected to vary with the intensity of competition in the habitat.

Veromessor pergandei is a xerophilous, seed-harvesting ant common in the deserts of southern California and Arizona as well as in Baja California and Sonora, Mexico (Creighton 1953). Mature colonies contain several thousand workers (Creighton 1953; Bernstein 1971; Went et al. 1972) that sometimes differ markedly from one another in size. The maximum variation in body length measured in this study is over twofold (3.5–8.4 mm). Where I have studied *V. pergandei*, it coexists with from one to four other granivorous species of the same subfamily (Myrmecinae). Food resources appear to limit populations of the desert seed-eating ants; both colony density and species diversity of these ants are highly correlated with mean annual precipitation, an index of seed production in the southwestern deserts (Davidson 1977). Within communities, body sizes of individual species are strongly correlated with the dimensions of experimental and native seeds foraged by these ants, and differences in body sizes are associated with resource subdivision and the structural organization of communities (Davidson 1977). Both Bernstein (1971) and Went et al. (1972) have observed that sizes of forage items appear to be proportional to morph sizes in *V. pergandei*. If worker body sizes in this species are adaptive because of their relative efficiencies at gathering certain sizes of food items, encounter rates with seeds of different dimensions should represent contingencies that select for particular caste ratios within colonies.

The purpose of this investigation is to relate resource exploitation by individual phenotypes of *V. pergandei* to the intensity of competition in the habitat. To accomplish this, I shall first demonstrate a relationship between niche breadth and the degree of worker size variability and then show that this variability is inversely correlated with the species diversity of granivorous ants in the local habitat.

METHODS

Sampling of Veromessor pergandei Workers

During the summers of 1974 and 1975, *Veromessor pergandei* workers were collected from seven populations in the deserts of southern California and southern Arizona (table 1). At each of these study locations, three to four apparently mature colonies were sampled by removing 30 workers per colony from foraging columns extending to seed baits within 5 m of the nest entrances. (Mature colonies are those which produce the reproductive castes. In the absence of any direct observations of reproductives, both large colony size and the presence of closely adjacent abandoned nest entrances used in previous foraging seasons were taken as indications of maturity.) Baits consisted of barley seeds, ground in a grain mill to produce a variety of sizes ranging from entire seeds and large fragments to fine powder. Seeds were presented to the ants in shallow glass ashtrays with strips of masking tape facilitating entry and exit of workers as in Brown et al. (1975). To avoid sampling biases, I traced a line across the foraging column in the sandy soil and collected all ants as they crossed this line. Workers were preserved in 70% ethanol and returned to the laboratory for measurement with a Wild M-5 binocular microscope and ocular micrometer.

TABLE 1

DESCRIPTIONS OF STUDY LOCATIONS AND MANDIBLE CHARACTERISTICS OF SAMPLED COLONIES

Location	Mean Annual Precipitation (mm)	Mean Mandible Length (mm)	Variability in Mandible Length (CV)
California, San Bernadino County, 8.5 km SE Baker, 287 m, July 26, 1974	76	.73 .73 .73	13.70 13.70 15.62
California, San Bernadino County, 11 km NNE Barstow, 659 m, July 30, 1974	88	.69 .72 .74 .76	10.23 9.82 12.09 14.41
California, Kern County, 1 km SE Mojave, 834 m, July 28, 1974	121	.80 .76 .78 .80	13.69 15.31 16.22 14.25
Arizona, Yuma County, 1.5 km S Tacna, 219 m, August 3, 1974	91	.76 .79 .74	11.01 9.81 14.17
Arizona, Maricopa County, 5 km SW Gila Bend, 225 m August 31, 1975	142	.83 .82 .82	12.64 14.43 9.45
Arizona, Pima County, 8 km N Ajo, 537 m, August 4, 1975	216	.79 .82 .80	9.81 9.45 10.46
Arizona, Pinal County, 8 km SSW Casa Grande, 425 m, August 30, 1975	215	.76 .73 .74	9.30 8.66 8.55

The dimensions of trophic appendages have frequently been shown to reflect prey sizes (reviewed by Hespeneheide 1973). I have chosen to use mandible length as an index of worker size that may be related to seed selection. Mandible lengths are very closely correlated with head lengths ($r = .85$), head widths ($r = .89$), and body lengths ($r = .81$) for 90 workers from Mojave, California, and are more easily and accurately measured (to 0.01 mm) than are dimensions of less sclerotized structures. Following Van Valen (1965), Grant (1971), and Rothstein (1973), I have computed the coefficient of variation as an estimate of variability in mandible length among workers of individual colonies (table 1). Throughout this paper, I define worker polymorphism by the amount of size variation within a colony.

Worker Size and Seed Utilization

To test for the postulated correlation between morph size and seed size selection, I employed the following procedures. In summer of 1974, I collected a number of returning workers from individual colonies in four of the seven study populations (table 2) and preserved them separately with the native forage items they transported. All collections were made from the distal ends of foraging columns to minimize any possible effect of distance on size preference (Davidson, in preparation). I measured ant mandibles and prey items in the laboratory to the nearest 0.01 mm and calculated an average of the two smallest seed dimensions (minimum cross-sectional area) as an

TABLE 2
RELATIONSHIPS BETWEEN WORKER MANDIBLE SIZE AND PREY SIZE FOR
FOUR *Veromessor pergandei* COLONIES FROM DIFFERENT SAMPLING LOCALITIES

Sampling locality	No.	<i>r</i>	<i>P</i> <
Barstow, Calif.	34	.52	.01
Mojave, Calif.	35	.52	.01
Tacna, Ariz.	39	.38	.05
Ajo, Ariz.	25	.29	NS

NOTE.—No. = the number of forage items (or mandibles) measured; *r* = the correlation coefficient in the regression of prey size on mandible size; *P* = the level of statistical significance corresponding to the value of *r*.

estimate of seed size. Because all *V. pergandei* workers can transport narrow objects of considerable length, seed widths apparently influenced foraging choices to a greater extent than did their lengths. In August of 1975 in Mojave, California, the relationship between mandible size and seed size selection was investigated experimentally, using seeds of uniform quality but different size. Pearl barley was ground in a grain mill and separated with Tyler sieves into four nonoverlapping and readily identifiable size classes based on cross-sectional area. Median diameters of these categories were size 1, 0.9 mm; size 2, 1.5 mm; size 3, 2.2 mm; size 4, 3.1 mm. I placed seed baits containing 2.5 g of each class of barley particles 8 m from each of two *V. pergandei* colonies and collected foraging workers in appropriately labeled vials denoting prey size choices. Mandibles of these ants were later measured in the laboratory.

Evaluation of the Competitive Environment

At each of the seven locations described in table 1, seed-eating ants were censused at bait stations using standard procedures in order to determine the relative intensity of interspecific competition. Eighty bait trays (as described above) were placed in an 8 × 10 bait grid with approximately 5-m spacing between stations. Because of the importance of soil temperatures in regulating activity patterns of desert ants (Bernstein 1974; Whitford and Ettershank 1975), I censused each bait for 60 s every 2 h for a full range of diurnal and nocturnal surface temperatures and noted the numbers of ants of each species that removed seed from the trays. Shannon-Wiener diversity indices ($H = -\sum p_i \ln p_i$) were computed for each census; values of p_i signify the proportion of the total number of seeds removed during the census by species *i*.

RESULTS

Relationship of Prey Size to Mandible Size

Table 2 shows that for three of the four colonies whose natural forage items were analyzed regressions of prey size on mandible length produced significant correlations. The fourth colony was sampled in Ajo, Arizona, where workers are less variable than at the other three sites represented here (table 1). In the food-choice experiments employing barley particles of different sizes, ants selecting seeds in each of the four size categories differed significantly ($F = 14.2$, $P < .005$) from one another in mandible length, with larger ants preferring larger seeds. Frequency distributions of mandible sizes for ants selecting seed sizes 1–3 are illustrated in figure 1. An insignificant number of workers chose seeds in the largest size category (size 4).

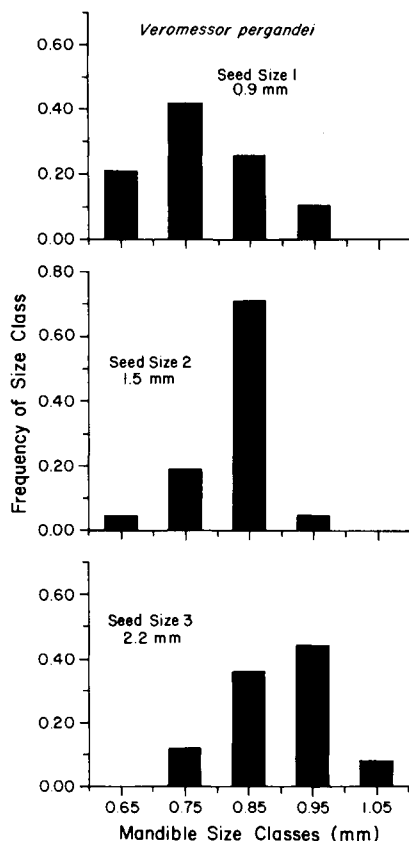


FIG. 1.—Frequency distributions of mandible size classes for 65 *Veromessor pergandei* workers foraging on barley seeds of three sizes from bait trays in Mojave, Calif.

Character Shifts in Relationship to Competition

Figure 2 describes the inverse and significant ($r = -.71$; $P < .01$) relationship between the within-colony coefficient of variation in mandible length and the species diversity of coexisting granivorous ants. Each point is based on measurements of 30 individual workers from a single colony, and workers were sampled from three to four colonies in each community. Figure 3 shows the frequency distributions of mandible size classes for *V. pergandei* workers in a number of the study locations; each graph represents the measurements of 90 ants. For habitats where additional species of granivorous ants coexist with *V. pergandei*, the body sizes of the next smallest and next largest species are indicated by arrows in this diagram. These data suggest that the distribution of worker sizes in *V. pergandei* is particularly responsive to those coexisting species that are most similar in body size.

DISCUSSION

Worker polymorphisms have evolved frequently during the phylogenetic history of the Formicidae, and castes have become specialized to varying degrees for one or more contingencies (Wilson 1953). Division of labor among worker castes has been studied

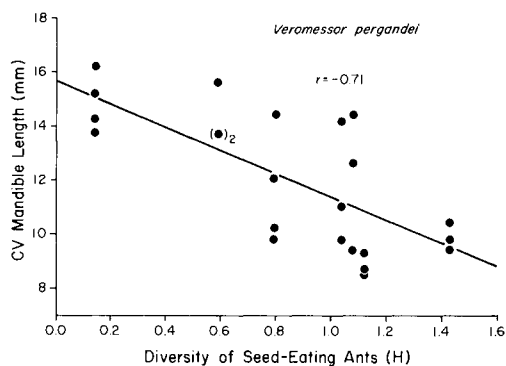


FIG. 2.—The relationship between the within-colony coefficient of variation in mandible length and the species diversity of seed-harvesting ants in the community ($r = -0.71$; $P < .01$). Each point includes the measurements of 30 workers from one colony.

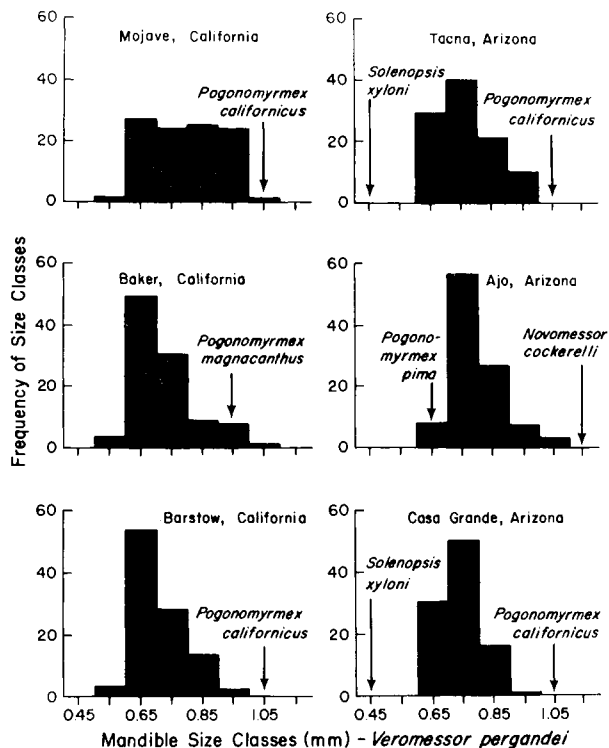


FIG. 3.—Frequency distributions of mandible size classes for *Veromessor pergandei* from six sampling locations. Mean mandible lengths of competitors most similar in size are indicated by arrows.

primarily within the context of single colonies. Variability in the expression of size polymorphism in *Veromessor pergandei* over its extensive geographic range provides a unique opportunity to assess the selective forces which may have influenced the extent of caste proliferation and specialization. The geographic range of this species includes the hottest and most arid deserts of North America; it extends from Death Valley south to central Baja California and eastward to south-central Arizona. Over much of this range, *V. pergandei* coexists with few other granivorous ants. Proximally, the limits of its distribution apparently correspond to habitat and elevational boundaries and probably reflect the operation of both physiological and ecological factors (Creighton 1953; Bernstein 1974). Ultimately, the success of *V. pergandei* in these harsh, unproductive areas may reflect its capacity to broaden its utilization of resources in the absence of competitors. Such plasticity may enable colonies to minimize overlap in prey size selection among foraging nestmates and thus to exploit the available diversity of seed sizes more efficiently.

Theory suggests that greater specialization in resource exploitation may be possible (MacArthur 1972) or even optimal (MacArthur and Pianka 1966; Emlen 1966) where resources are more abundant, if the diversity of resources remains the same. In more mesic habitats, where seed production may be enhanced over the entire range of seed sizes, granivorous ant communities include a greater proportion of species whose workers are relatively monomorphic in size (Davidson 1977). In the most productive deserts and the even more productive desert grasslands *V. pergandei* is replaced by species such as *Pogonomyrmex rugosus* and *P. barbatus*, which have slightly larger and more uniform sized workers but generally similar ecologies.

The data presented here imply that competition may constrain diet breadth in *V. pergandei* and select for accompanying morphological change within colonies. In this species, the degree of within-colony worker size polymorphism is highly correlated with an estimate of the intensity of interspecific competition. Both observations and experiments confirm that the various castes of *V. pergandei*, foraging from similar seed distributions, tend to take different sizes of seeds. Therefore, colonies displaying the most variability in worker size should have the greatest diet breadth. It could be argued that diet breadth is also enhanced by increasing the average worker size. Mean mandible size of workers does vary among local populations (table 1); this variability is slight and apparently unrelated ($r = .39$, $P > .05$) to the diversity of competing species.

Shifts in the caste ratios of *V. pergandei* between sampling sites (fig. 3) are generally consistent in magnitude and direction with their interpretation as responses to competition for food with coexisting species of similar size and trophic specialization. Workers are most uniformly distributed among size classes in Mojave, California, where the single coexisting granivorous ant, *Pogonomyrmex californicus*, is rare. At the remaining locations, where *P. californicus* or species of similar large body size occur in greater relative abundance, the proportion of large morphs in *V. pergandei* populations is substantially reduced. In the three Arizona sites shown in figure 3, the presence of smaller seed-eating competitors is accompanied by a considerable reduction in the proportion of smaller castes (those with mandible lengths in the size classes centered at 0.55 and 0.65 mm). In Ajo, where *P. pima* (mean mandible length of 0.64 mm) coexists with *V. pergandei*, this effect is particularly apparent.

An alternative hypothesis might ascribe differences in worker size distributions in *V. pergandei* primarily to variability in the plant community and, consequently, in the diversity of seed sizes produced in local habitats. Measurements of the relative abundances of seeds in various size classes would be difficult to obtain with confidence for so many habitats where communities of annual plants and seed levels in soils fluctuate dramatically over seasons and years. However, the presence of additional species of both

smaller and larger worker body sizes where similar-sized morphs of *V. pergandei* are less abundant (fig. 3) makes it unlikely that the decline in polymorphism in this species simply reflects reduced diversity in the sizes of seeds produced locally. Elsewhere (Davidson 1977), I show that for these additional species seed size selection is also strongly correlated with worker body size.

Proximate mechanisms of caste determination are, in general, poorly understood (reviewed in Wilson 1971), and it is not clear how caste ratios are proximately regulated in *V. pergandei*. Short-term as well as long-term adjustments may be possible. Caste ratios in foraging columns might differ from those of worker populations in the colony as a whole and change with local or seasonal variations in seed availability. Some of the variability in figure 2 may be related to such factors. However, all of these data are based on collections of *V. pergandei* during the months of July and August (though in two different years), and none of the colonies were sampled during seed production periods in their respective habitats. Sampling of workers at uniform baits located at approximately the same distances from nest entrances should also have helped to minimize any potential bias related to differential recruitment to rewards of unequal value.

To some extent, ants and other social insects may resolve interspecific interactions differently than do other types of organisms, simply because different options are available to them. Culver (1974) has argued convincingly that behavioral plasticity may strongly influence the outcome of interspecific competition in ants and that the same species may play different functional roles in different communities. The relationship between worker size polymorphism in *V. pergandei* and the intensity of competition in the environment illustrates that morphological plasticity related to the variance of resources utilized by individual phenotypes (colonies) may be important as well. Among many types of organisms, an individual can become a generalist only by compromising its fitness as a specialist. For example, by increasing its body size where larger competitors are absent, a solitary predator may be capable of subduing prey in a greater variety of size classes but become less efficient at exploiting small prey and may no longer be able to utilize certain microhabitats. In social insects such as *V. pergandei*, a finer degree of adaptation may be possible if natural selection acts approximately so as to maximize the overall foraging efficiency of the colony. When competitive pressures are reduced, colonies may expand their utilization of resources without sacrificing efficiency by producing different worker castes in frequencies to match the distribution of available resources.

In *V. pergandei*, morphological plasticity appears to be associated primarily with exploitative competition, but the potential exists for caste ratio shifts in response to other ecological interactions as well. Among many ants, competition proceeds by interference rather than exploitative mechanisms (Levins et al. 1973; Culver 1974). For polymorphic species in which different castes participate unequally in interference interactions, caste ratios may respond to variability in the intensity of interference competition. The potential should also exist for modification of caste ratios on the basis of predation or parasitism if either or both of these sources of mortality fall disproportionately on particular castes in polymorphic species.

SUMMARY

Worker size polymorphism in colonies of *Veromessor pergandei*, a granivorous desert ant, is inversely related to the intensity of interspecific competition in the habitat for seven ant communities in the deserts of southern California and southern Arizona. Seed size preferences are positively correlated with worker body sizes, and diet breadth relative to seed size is probably enhanced by colony polymorphism. Niche shifts within

colonies of these social insects may permit unusually fine adaptation to the resource environment. In contrast to solitary organisms, for which generalization of the diet may imply significant trade-offs, these ants may expand their utilization of resources where competitors are absent while retaining an efficient size match to the distribution of available resources.

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